A predator in need is a predator indeed: generalist arthropod predators function as pest specialists at the late growth stage of rice

Gen-Chang Hsu[1], Jia-Ang Ou[2,3], Min-Hsuan Ni[2], Zheng-Hong Lin[2] and Chuan-Kai Ho[1,2*]

[1]Department of Life Science, National Taiwan University, Taipei, Taiwan

[2]Institute of Ecology and Evolutionary Biology, National Taiwan University, Taipei, Taiwan

[3]Department of Zoology, University of British Columbia, Vancouver, Canada

* Corresponding author. ORCiD ID: http://orcid.org/0000-0002-6437-0073 Email: ckho@ntu.edu.tw

Abstract

Biocontrol, using natural enemies for pest control, has a long history in agriculture. It has received a surge of interest in the recent Anthropocene because of its potential as a valuable tool for sustainable agriculture. To solve a long-standing puzzle—how well the ubiquitous generalist arthropod predators (GAPs) function as biocontrol agents—we used stable isotope analysis to quantify their diet composition in organic and conventional rice farms over crop stages in three consecutive years. We found that the proportion of rice pests in GAPs' diets increased toward late crop stages and consistently reached 79-95% at the ripening stage over three years (with different climatic conditions) in both organic and conventional farms. This consistently high percentage in pest consumption indicates that GAPs could function as pest specialists during the critical period of crop production, providing support for the use of GAPs in pest management for sustainable agriculture.

Keywords: biocontrol, rice herbivores, pest, detritivores, diet composition, pest management, predator-prey interactions, trophic interactions, generalist predators, rice paddy, organic and conventional farms, crop stage, stable isotope analysis

Introduction

Using natural arthropod enemies for pest control has a long history in agriculture. The earliest record of biocontrol was documented in the book *Plants of the Southern Regions* (*ca.* 304 A.D.). It described people in Southern China selling ants and their nests (attached to branches) in the markets to control citrus insect pests[1]. Nevertheless, with the advent of modern technologies in the past century, synthetic pesticides have become the main method for controlling pests in agriculture. However, this comes at a cost, such as posing risks to people, reducing biodiversity (e.g., a decline in top predators) and hampering ecosystem functions (e.g., a decline in pollinator service) [2,3]. As agriculture has become the largest land use type worldwide and a major driver for the global biodiversity crisis and environmental degradation in Anthropocene [4], a shift from synthetic pesticides to environmentally friendly practices (e.g., biocontrol) is urgently needed to make agriculture more sustainable [5]. For example, the European Commission has recently announced its plan to reduce the use of chemical pesticides in European Union agricultural systems by 50% by 2030 [6]. To achieve this ambitious sustainability goal, biocontrol by natural enemies has been considered a key approach and has regained importance in modern agriculture.

Natural enemies used for pest control can be classified into two major groups based on their prey range: specialist and generalist predators. While specialist predators (e.g., parasitoid wasps) have been widely advocated in agriculture because they target specific pest species and produce less undesirable non-target effects [7], generalist predators (e.g., spiders) have been increasingly appreciated for their conspicuous existence and consistent biocontrol effect on pests [7-10]. For example, generalist predators were commonly reported in various agro-ecosystems and significantly reduced pest abundances in approximately 75% of cases in 181 field manipulative

studies [8]. Moreover, a meta-analysis suggests that generalist predators may exert stronger biocontrol effects on pest populations over time compared to specialists [7].

While the value of generalist predators has been increasingly appreciated, a few fundamental knowledge gaps need to be filled to validate their biocontrol potential and the underlying mechanisms in agro-ecosystems. For example, while studies have qualitatively analyzed the diets of generalist predators (e.g., using molecular gut content analysis to identify prey species) [11-13], very few have quantified their diet composition over a growth season in the field (knowledge gap 1) [10]. Quantifying their diet composition will provide critical information to address the concern that generalist predators may switch their diet from pests to alternative prey and thus reduce their pest control effectiveness [9]. For instance, if generalist predators still consume a high proportion of pests in their diet with the presence of alternative prey in the field, this result would help end a long debate on whether generalist predators serve well as biocontrol agents [8,9,14]. Moreover, examining the consistency of generalist predators in pest consumption in the field over years is important to assess the reliability of these predators as biocontrol agents in agriculture, although this information is lacking (knowledge gap 2). Given that dynamics in population density or species composition commonly occur in agro-ecosystems [15,16], a consistently high pest consumption by generalist predators over years, if it occurs, will provide strong support for applying these predators in pest management programs.

To better understand the underlying mechanisms for the biocontrol effect of generalist predators, we also need to examine how various abiotic and biotic factors affect the diet composition of generalist predators in agro-ecosystems (knowledge gap 3). First, arthropod community composition (e.g., pest vs. alternative prey density) may vary with crop stages over the growth season and affect predator-prey trophic interactions [17]. Therefore, we should examine

how crop stage affects the pest consumption by generalist predators to understand whether the role of these predators as biocontrol agents varies within a growth season. Second, we should examine whether farming practices (e.g., organic and conventional) influence the diet composition of predators (e.g., pest consumption) [18]. This will demonstrate whether generalist predators provide varying biocontrol values in specific farm types. In general, compared to conventional farming, organic farming promotes arthropod diversity (both pest and alternative prey) [19], potentially lowering the pest consumption by generalist predators [10]. In contrast, the application of synthetic chemicals in conventional farms may promote pest abundance [16,20-22], potentially leading to higher pest consumption by predators. Third, we should investigate the relationship between the relative prey abundance and the diet composition of their predators. This will clarify whether pest abundance or predator preference mainly explains the pest consumption by predators [17, 23-25]. Lastly, we should examine how surrounding vegetation (e.g., forest cover) affects the diet composition of generalist predators. While surrounding vegetation reportedly affected arthropod diversity and predator-prey interactions in agro-ecosystems [26-30], its effect on predators' diet composition is unclear. Understanding this will provide insights for managing the agricultural landscape and promoting biocontrol services by generalist predators.

To address these three knowledge gaps, this study aimed to 1) quantify the diet composition of generalist predators, 2) examine the consistency of predators in pest consumption over years, and 3) investigate how abiotic and biotic factors affect the diet composition of these predators. Filling these gaps will provide insights for applying generalist predators in biocontrol programs. Specifically, this study sampled arthropod prey and generalist arthropod predators (GAPs) in sub-tropical organic and conventional rice farms over the rice growth season (seedling, tillering, flowering, and ripening stages) in Miaoli County, Taiwan from 2017 to 2019. The

objectives of this study were to 1) quantify the diet composition of GAPs (ladybeetles and spiders) at each rice stage using stable isotope analysis ($\delta^{13}C$ and $\delta^{15}N$), 2) examine GAPs' consistency in pest consumption over years (i.e., the proportion of rice pests in GAPs' diets in 2017-2019), and 3) investigate how local abiotic and biotic factors (e.g., farm type, crop stage, percent forest cover, and the relative abundance of pests in the field) may affect pest consumption by GAPs. Stable isotope analysis has been widely applied in ecology to infer predator-prey trophic interactions and estimate the proportion contribution of different prey sources to predators' diets [31-33]. This quantification method reflects accumulated prey consumption in predators' diets, which may not be achieved by some "snap-shot" techniques (e.g., field observations and molecular gut content analysis) [34]. We found that predators (GAPs) consumed a high proportion of rice pests in their diet at late crop stages (e.g., 79-95% at the ripening stage in all rice farms during 2017-2019). Such high pest consumption patterns were similar across the three study years, suggesting that i) the top-down control of pests by generalist predators was consistent over years, and ii) generalist predators may function as "specialist predators" of pests at late crop stages (when pests are abundant). Moreover, predators in conventional farms consumed a higher proportion of rice pests than those in organic farms. By quantifying the diet composition of GAPs over crop stages and years, our study lends support to applying generalist predators as biocontrol agents in both organic and conventional rice farms. To promote sustainable agriculture, we encourage studies to investigate whether generalist predators may commonly function as "specialist predators" of crop pests in various agro-ecosystems.

Materials and Methods

Study system and sample collection

We collected terrestrial arthropods in organic and conventional rice farms in subtropical Taiwan (latitude and longitude ranges) from 2017 to 2019 (three farms each in 2017 and seven farms each in 2018 and 2019). These farms, averaged at 0.2 hectares, were irrigated with surface water. The organic farms were managed with organic fertilizers (manure; 2-3 applications/crop season) and natural pesticides (tea saponins; 1 application/crop season). The conventional farms were managed with synthetic nitrogen fertilizers (2-3 applications/crop season) and organophosphate pesticides (1 application/crop season). At each major rice crop stages (seedling, tillering, flowering, and ripening stage) during the growing season (April - July) in each study year, we collected arthropod samples by sweep-netting (36 cm in diameter with a mesh size of 0.2 × 0.2 mm) the crop canopy 60 times along the farm ridges. Samples were sealed in bags without chemical preservatives, iced, and transferred to refrigerator (−20ºC) in the laboratory. We identified and counted arthropods under a dissecting scope to the lowest possible taxonomic level. Main orders, families, and genera have been documented in Hsu et al. [10].

Stable isotope analysis of arthropod samples

After identification, arthropod samples were prepared for stable isotope analysis. First, samples were oven dried (50ºC) for one week, ground, and weighed into individual tin capsules (5 × 9 mm). If necessary, several conspecifics would be pooled into a capsule to meet the minimum weight required for stable isotope analysis (i.e., 2 mg in this study). Stable isotope analysis was conducted at the UC Davis Stable Isotope Facility using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). The standards for carbon and nitrogen stable isotope ratios were Vienna PeeDee

Beleminte and atmospheric N_2, respectively. The results of our samples were expressed in per mil (‰) relative to the international standards ($\delta^{13}C$ and $\delta^{15}N$).

Arthropod trophic guild assignment

A trophic guild represents a group of species using similar resources and forms a basic component of food webs. The concept has been proved to be practical in current ecology because it condenses broad taxonomic information into distinct functional groups in communities [35]. In this study, we classified arthropod samples into four trophic guilds based on their dietary information and isotope signatures [10]: 1) "Predators" consisted of spiders and ladybeetles, which are the primary GAPs in rice farms. 2) "Rice herbivores" consisted of major rice pests, including planthoppers, leafhoppers, and stink bugs. 3) "Tourist herbivores" consisted of herbivorous species without direct trophic association with rice plants, including some grasshoppers and leaf beetles. 4) "Detritivores" consisted of arthropods that feed on decaying organic material or plankton, including various midge and fly species. The arthropod families/genera in each trophic guild are detailed in Appendix S1: Table S1. This study focused on the trophic interactions between generalist predators and their prey sources and therefore did not consider less abundant trophic guilds (e.g., parasitoids) in subsequent analyses.

Data analyses

To quantify the diet composition of predators, we constructed a Bayesian stable isotope mixing model using the R MixSIAR package [36] to estimate the proportions of different prey sources (i.e., the three prey guilds including rice herbivores, tourist herbivores, and detritivores) in predators' diet. In the mixing model, individual farm-year combination and crop stage were included as

fixed effects for predator isotope data to examine their effects on predators' diet composition; isotope data for the three prey guilds were pooled respectively to generate fixed source values due to their high mobility across farms [37,38]. Isotope data at the seedling stage for the three study years were omitted from the analysis due to insufficient sample sizes for model estimation. To improve our model estimates, carbon and nitrogen concentration dependencies as well as the residual/process errors were incorporated [36,39]. Trophic discrimination factors (TDFs) were estimated from the diet-dependent discrimination equation proposed by Caut, et al. [40]. We ran three Markov Chain Monte Carlo (MCMC) chains, each with 50,000 iterations and a burn-in number of 25,000, along with a non-informative Dirichlet prior. Chain convergence was assessed via Gelman-Rubin and Geweke diagnostics. Bayesian posterior mean estimates of diet composition (for each farm-year-stage combination) were extracted for further analysis.

To examine how local abiotic and biotic factors (e.g., farm type, crop stage, percent forest cover, and the relative abundance of pests in the field) may affect the pest consumption by GAPs, we first fit beta regression models with year, farm type, crop stage, percent forest cover, and the relative abundance of rice herbivores as fixed effects without interactions and the proportion of rice herbivores consumed in predators' diet as the response variable using the R betareg package [41]. We then refit the first model by adding the interaction terms among all the significant factors to create the final model. Model parameters were estimated using maximum likelihood, and their significance was analyzed using the "Anova" function in the R car package [42]. Tukey's post-hoc tests were performed for the significant factors using the "cld" function in the R emmeans package [43]. Note that the percent forest cover around each study farm was estimated from Google Earth images by manually delimiting the forested areas within a 1-km radius circular buffer surrounding the farm and computing the fraction of these areas in the

187 buffer zone. Because spiders and ladybeetles were the most abundant generalist predator groups
188 in our study system and exhibited distinct foraging behavior (e.g., sit-and-wait vs. active
189 hunting), we also performed all the aforementioned analyses separately for each of the two
190 predator groups. All analyses were conducted in R version 4.0.3 [44].
191
192 **Results**
193 *Diet composition of predators in rice farms*
194 Across organic and conventional farms during 2017-2019, the proportion of rice herbivores in all
195 predators' diet increased over the course of the crop season from 23-47% at the tillering stage to
196 79-95% at the ripening stage; the proportion of detritivores in predators' diet decreased from 38-
197 59% at the tillering stage to 1-2% at the ripening stage; the proportion of tourist herbivores in
198 predators' diet also decreased from 15-22% at the tillering stage to 4-19% at the ripening stage
199 (Fig. 1a; Appendix S1: Table S2).
200 Regarding individual predator groups, spiders and ladybeetles showed a marked
201 difference in their diet composition over crop stages during 2017-2019. Across organic and
202 conventional farms, spiders consumed a higher proportion of detritivores (33-55%) in their diet
203 in the beginning of crop season (tillering stage) and substantially increased the consumption on
204 rice herbivores to 78-94% in late crop season (ripening stage) (Fig. 1b; Appendix S1: Table S2).
205 In contrast, ladybeetles in both organic and conventional farms consumed a low proportion of
206 detritivores (≤ 17%) and a steadily high proportion of rice herbivores (≥ 74%) in their diet
207 throughout the crop season (Fig. 1c; Appendix S1: Table S2). For both predator groups, tourist
208 herbivores generally did not constitute an important prey source and contributed less than 33% to
209 the predators' diet (Fig. 1b, 1c; Appendix S1: Table S2).

210

211 *Patterns of rice herbivore consumption by predators*

212 We further analyzed rice herbivore consumption by GAPs since these herbivores are the main
213 pests of concern. The patterns of rice herbivore consumption by all predators in organic and
214 conventional rice farms were generally similar across the three study years, suggesting
215 consistency in GAPs' feeding habits (Fig. 2). The consistency in herbivore consumption over
216 years was also revealed by our beta regression model, which indicated that the proportion of rice
217 herbivores consumed in all predators' diet did not vary across years ($\chi^2 = 1.99$, $P = 0.37$; Table
218 1).

219 Interestingly, spiders and ladybeetles exhibited distinct within-season patterns of rice
220 herbivore consumption. For spiders in organic and conventional farms, the proportion of rice
221 herbivores in their diet increased toward later crop season, ranging from 20-48% (tillering) to 78-
222 94% (ripening) (Fig. 2b; Appendix S1: Table S2), whereas for ladybeetles in organic and
223 conventional farms, the proportion of rice herbivores in their diet remained relatively stable
224 throughout the season, ranging from 74-85% (tilling) to 93-95% (ripening) (Fig. 2c; Appendix
225 S1: Table S2).

226

227 *Factors associated with rice herbivore consumption by predators*

228 The proportion of rice herbivores in GAPs' diet differed between organic and conventional farms
229 (All predators: $\chi^2 = 15.98$, $P < 0.001$; Spiders: $\chi^2 = 13.38$, $P < 0.001$; Ladybeetles: $\chi^2 = 6.70$, $P =$
230 0.001; Table 1). Specifically, all predators consumed a higher proportion of rice herbivores in
231 their diet in conventional vs. organic farms (Tukey's post-hoc test, $P < 0.05$; Table 2), although
232 spiders' diet was affected by a farm type-year interaction ($\chi^2 = 7.64$, $P = 0.02$; Table 2).

233 The proportion of rice herbivores in GAPs' diet also differed among crop stages (All
234 predators: $\chi^2 = 227.93$, $P < 0.001$; Spiders: $\chi^2 = 115.43$, $P < 0.001$; Ladybeetles: $\chi^2 = 152.60$, $P <$
235 0.001; Table 1). Specifically, GAPs consumed higher proportions of rice herbivores in their diet
236 at the flowering and/or ripening stage vs. the tillering stage (Tukey's post-hoc test, $P < 0.05$;
237 Table 3).
238 Different from previous studies showing the importance of surrounding landscape in
239 determining arthropod community structure and pest control by predators [45] , but see [46], this
240 study found no correlation between proportion of rice herbivores in GAPs' diet and the percent
241 forest cover within a 1-km radius buffer surrounding the study farms (All predators: $\chi^2 = 0.30$, P
242 = 0.58; Spiders: $\chi^2 = 1.28$, $P = 0.26$; Ladybeetles: $\chi^2 = 0.77$, $P = 0.38$; Table 1). Furthermore, the
243 proportion of rice herbivores consumed was not associated with the relative abundance of rice
244 herbivores in the field (All predators: $\chi^2 = 0.36$, $P = 0.55$; Spiders: $\chi^2 = 1.38$, $P = 0.24$;
245 Ladybeetles: $\chi^2 = 0.93$, $P = 0.33$; Table 1).
246
247 **Discussion**
248 Because the worldwide demand for environmentally friendly practices in agriculture has
249 increased, we investigated the potential of GAPs (ubiquitous in nature) as biocontrol agents in
250 agro-ecosystems. Specifically, we used stable isotopes to quantify the diet composition of GAPs
251 in organic and conventional rice farms during the crop season in three consecutive years. Our
252 main results include the following: 1) Across the three study years, the rice herbivore
253 consumption by GAPs increased in both organic and conventional farms over the crop season,
254 from 23-47% at the tillering stage to 79-95% at the ripening stage (Fig. 1a). The high percentage
255 at the ripening stage indicates that GAPs could function as specialists in pest management during

256 critical growth (late crop) stages. Notably, rice herbivore consumption by spiders increased
257 gradually toward the later crop season (Fig. 2b), whereas the consumption by ladybeetles
258 remained stable throughout the season (Fig. 2c). 2) Our results revealed similar among-year
259 patterns in rice herbivore consumption by GAPs in organic and conventional rice farms,
260 suggesting a consistency in GAP feeding habits and biocontrol value (Fig. 2, Table 1). 3) The
261 proportion of rice herbivores in GAPs' diets varied with farm type and crop stage (e.g., higher in
262 conventional farms and during flowering/ripening stages). However, contrary to results from
263 previous studies, pest consumption by GAPs was not associated with surrounding landscape (e.g.,
264 percent forest cover) or the relative abundance of rice herbivores in the field (Table 1). We
265 discuss in the following: 1) GAPs function as specialists at late crop stages, 2) GAPs exhibit
266 consistent pest consumption patterns over years, 3) factors associated with pest consumption by
267 predators, and 4) the potential caveats of this study. We finish by highlighting the implications
268 of our results for agricultural management.
269
270 *1) Generalist predators function as specialists at late crop stages*
271 While biocontrol, a farming practice with a long history, offers a promising solution for
272 sustainable agriculture, the use of GAPs as biocontrol agents remains a concern because GAPs
273 may switch diets between pests and alternative prey [47-49]. This study addressed this concern and
274 revealed a consistency in high pest consumption by GAPs at late crop stages over years. The
275 results provide not only strong support for using GAPs in sustainable pest management, but also
276 a novel aspect in biocontrol—generalist predators may function as specialist predators of pests
277 during the late crop season. Specifically, across the three study years, GAPs in both organic and
278 conventional farms consumed an increasing proportion of rice herbivores over the crop season,

279 reaching 79-95% in predators' diet at the ripening stage, whereas the proportions of alternative
280 prey (detritivores and tourist herbivores) in their diet gradually decreased below 21% at the
281 ripening stage (Fig. 1, Appendix S1: Table S2). The increase in rice herbivore consumption over
282 time suggests that the biocontrol potential of predators increases toward late crop stages and
283 peaks at the critical stage of crop production. This could be because of a higher herbivore (pest)
284 density at late crop stages, suggested by a correlation between rice herbivore consumption and
285 crop stage (see *Factors associated with pest consumption by predators*).

286 While GAPs consumed a high proportion of pests at late crop stages, the two predator
287 groups in our study system, spiders and ladybeetles (Table S1), exhibited distinct dietary patterns
288 over the crop season (Fig. 1, Fig. 2). Specifically, pest consumption by spiders increased
289 substantially, but pest consumption by ladybeetles remained stable over the season (Fig. 2b vs.
290 2c). This may be because different foraging modes—sit-and-wait (spiders) or actively hunting
291 (ladybeetles)—can lead to different prey capture and thus diet composition [50,51]. For example,
292 long-jawed orb-weavers (Tetragnathidae), the most abundant family in our spider samples, are
293 sit-and-wait predators. The diet composition of these predators may correlate with prey
294 abundance [50]. In fact, spiders' diet composition appeared to correlate with prey abundance in
295 this study (Fig. 1b, Fig. 3), although crop stage, rather than pest abundance, better predicted the
296 pest consumption by predators (see *Factors associated with pest consumption by predators*). In
297 contrast, ladybeetles are actively hunting predators and may preferentially feed on rice
298 herbivores, resulting in stable pest consumption over time (Fig. 1c, Fig. 2c, Fig. 3). Because
299 predator foraging modes shape predator-prey-plant interactions [52], we suggest future studies to
300 examine different assemblages of sit-and-wait vs. actively hunting predators in field conditions
301 to reveal the most efficient biocontrol practice over the entire crop season.

2) Generalists exhibit consistent pest consumption patterns over years

Ideal biocontrol agents provide a consistent, predictable effect on pests under various environmental conditions. Accordingly, GAPs in this study showed consistent pest consumption across years (Fig. 2), despite various abiotic and biotic environmental conditions. Specifically, regarding the abiotic factors, the daily mean temperature, particularly from April to June, varied substantially among years (Appendix S1: Fig. S2). The daily precipitation also fluctuated over the three study years, with multiple high precipitation events in 2017, overall low precipitation in 2018, and relatively uniform precipitation in 2019 (Appendix S1: Fig. S2). Regarding the biotic factors, the composition of rice herbivores at the flowering and ripening stages differed substantially among the three years, in particular the two most dominant groups: leafhoppers (Cicadellidae/*Nephotettix*) and planthoppers (Delphacidae/*Nilaparvata*) (Appendix S1: Table S3). Although both abiotic and biotic factors varied substantially over the years of our study, pest consumption by GAPs generally remained stable, suggesting that GAPs can be a predictable, valuable tool for pest control in sustainable agriculture, but see [53].

3) Factors associated with pest consumption by predators

The proportion of rice pests in GAPs' diets differed between farm types and among crop stages but was not associated with the percent forest cover surrounding the farms or the relative abundance of rice herbivores in the field (Table 1). Overall, GAPs in conventional farms consumed a higher proportion of rice pests in their diet compared with those in organic farms (Table 2). There may be two explanations for this: 1) Organic farming may promote arthropod diversity and therefore distract predators from feeding on target pests [19,30,54]. 2) Pest densities

may be higher in conventional farms [55], thus leading to higher predator-prey encounter rates and pest consumption by GAPs. Regardless of the potential mechanisms, our results highlight the important but overlooked biocontrol value of GAPs in conventional farming systems.

Besides farming practices, the crop stage also affected pest consumption. Overall, pest consumption by GAPs increased from early (tillering) to late (ripening) stages (Fig. 2, Table 3), consistent with previous studies where predators consumed more pests in the late crop season [10,17]. The underlying mechanisms in our study may be summarized as follows: low pest density at the early crop stage led to low pest consumption by GAPs; however, pest populations increased with rice development and eventually predominated, leading to high pest consumption by GAPs at the flowering and ripening stages (Fig. 2 and 3). These findings indicate a higher biocontrol value of predators during the middle and late crop seasons, when the crop production is most vulnerable to pest damage. Therefore, farming practitioners may want to avoid practices that harm predators (e.g., chemical applications) during this period to maintain healthy predator populations and associated ecosystem services.

While habitat structure (e.g., surrounding vegetation) critically affects predator abundance and diversity [26,28-30], its effect on the diet composition of predators remains unclear. Complex surrounding vegetation has been suggested to promote predator abundance and diversity [26,56], but such higher complexity did not affect predators' diet composition in our study (Table 1). This might be because the prey species in our study system were mostly associated with rice plants but not the surrounding vegetation, consistent with a meta-analysis where habitat complexity had no effect on crop herbivore densities [56]. Nevertheless, increasing vegetation complexity remains an important topic because it could benefit pest control by enhancing predator density and diversity.

Notably, although the diet composition of generalist predators correlated with prey availability in the field [10,25], our beta regression model suggests no such correlation between rice herbivores and GAPs (Table 1). An explanation is that the relative abundance of rice herbivores was highly correlated with crop stage, a significant factor likely associating with various covariates (e.g., rice plant height) and explaining most variations (Fig. 3, Table 1). We encourage further experiments, both observational and manipulative, to clarify the link between prey availability and generalist predators' diet composition in the field.

4) Potential caveats of this study

Our study demonstrates high pest consumption by GAPs in rice fields over three years and examines the factors influencing GAPs' diet composition. While our study provides evidence for GAPs' biocontrol potential, some caveats may exist. First, high pest consumption in GAPs' diets does not necessarily imply a strong suppression of pest populations in the field, since pest population dynamics depend not only on the per capita effect of predators but also predator density and diversity [45,57]. To unveil the connection between per capita pest consumption and overall pest dynamics, future work may require complementing stable isotope analysis with field observations of predator and pest populations. Second, while intra-guild predation potentially influences the pest control by GAPs [9,58], it was not accounted for in our diet composition analysis due to the limitation of stable isotope mixing models [10]. However, this may not be a major concern in our study because rice plants grow as dense clumps and form a complex structure that could substantially relax intra-guild predation pressure [59,60]. Regardless, we caution that our diet estimates of predators (without predator-predator interference) might not apply to systems where intra-guild predation prevails.

Conclusions

While biocontrol has been recognized as a valuable tool for sustainable agriculture, whether generalist predators can serve as effective biocontrol agents in pest management remains unclear. Our study helps solve this long-standing puzzle by quantifying the diet composition of GAPs and identifying the underlying mechanisms for enemy-pest interactions in rice farms over three consecutive years. The results show a high proportion of rice pests in GAPs' diets in both organic and conventional farms (e.g., 79-95% at the ripening stage), suggesting that these generalist predators function as "specialist predators" at late crop stages (when rice plants are fruiting and pests are abundant). The high pest consumption remained consistent across years regardless of climatic conditions, demonstrating the potential that generalist predators may produce a stable, predictable top-down effect on pests. As sustainable agriculture has become more important than ever in human history, incorporating the ubiquitous generalist predators into pest management will open a promising avenue towards this goal.

Data availability

The source data to generate all figures and tables in the main text and the supplementary information will be available in Figshare with data DOI: xxx.

Acknowledgements

We thank Steven C. Pennings for constructive comments, and Yu-Pin Lin, Chih-Wei Tsai, Chi-Lun Huang, Su-Chen Chang, Hung-Ju Chen, C.-Y. Ho, F.-J. Sha, Y.-C. Chung, K.-C. Ho, and H.-C. Ho for logistic supports. We appreciate the Miaoli District Agricultural Research and Extension Station for field assistance, and the Council of Agriculture, Executive Yuan, Taiwan (106AS-4.2.5-ST-a1, 107AS-4.2.3-ST-a1, 108AS-4.2.2-ST-a1, 109AS-4.2.2-ST-a1) and the National Science and Technology Council (108-2621-B-002-003-MY3, 111-2621-B-002-003-MY3) for funding support.

Author Contributions

All authors conducted the experiments; G.-C. Hsu and C.-K. Ho designed and wrote the manuscript; G.-C. Hsu and J.-A. Ou performed the statistical analyses.

Competing Interests

The authors declare no competing interests.

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Table 1. Statistical results from beta regression models for examining the effects of abiotic and biotic factors on pest consumption by all predators, spiders, and ladybeetles. Interactions were tested only between significant factors within each model.

Model	Factor	*d.f.*	χ^2	*P*
All predators	Year	2	1.99	0.37
	Farm type	1	15.98	< 0.001
	Crop stage	2	227.93	< 0.001
	Percent forest cover	1	0.30	0.58
	Relative abundance of rice herbivores	1	0.36	0.55
	Farm type × Crop stage	2	2.06	0.36
Spiders	Year	2	7.92	0.02
	Farm type	1	13.38	< 0.001
	Crop stage	2	115.43	< 0.001
	Percent forest cover	1	1.28	0.26
	Relative abundance of rice herbivores	1	1.38	0.24
	Year × Farm type	2	7.64	0.02
	Year × Crop stage	4	0.99	0.91
	Farm type × Crop stage	2	1.12	0.57
	Year × Farm type × Crop stage	4	0.44	0.98
Ladybeetles	Year	2	13.20	0.001
	Farm type	1	6.70	0.001
	Crop stage	2	152.60	< 0.001
	Percent forest cover	1	0.77	0.38
	Relative abundance of rice herbivores	1	0.93	0.33
	Year × Farm type	2	5.78	0.06
	Year × Crop stage	4	6.80	0.15
	Farm type × Crop stage	2	1.95	0.38
	Year × Farm type × Crop stage	4	2.37	0.67

548 **Table 2.** Tukey's post-hoc tests comparing the proportion of rice herbivores consumed in the
549 diet of predators in organic and conventional rice farms. Different superscript letters indicate
550 significant differences in the means ($\alpha = 0.05$) within each model.

Model	Farm type	Mean (± SE)	Lower 2.5%	Upper 2.5%
All predators	Organic	0.66^{a} (± 0.02)	0.63	0.69
	Conventional	0.73^{b} (± 0.01)	0.70	0.76
Spiders	Organic	0.64^{a} (± 0.02)	0.60	0.68
	Conventional	0.73^{b} (± 0.02)	0.69	0.77
Ladybeetles	Organic	0.86^{a} (± 0.01)	0.85	0.87
	Conventional	0.88^{b} (± 0.01)	0.87	0.89

551

552

553 **Table 3.** Tukey's post-hoc tests comparing the proportion of rice herbivores consumed in the
554 diet of predators at three crop stages (tillering, flowering, and ripening stage). Different
555 superscript letters indicate significant differences in the means ($\alpha = 0.05$) within each model.

Model	Crop stage	Mean (± SE)	Lower 2.5%	Upper 2.5%
All predators	Tillering	0.32^{a} (± 0.03)	0.27	0.38
	Flowering	0.84^{b} (± 0.02)	0.81	0.87
	Ripening	0.92^{c} (± 0.01)	0.90	0.95
Spiders	Tillering	0.35^{a} (± 0.04)	0.28	0.42
	Flowering	0.82^{b} (± 0.02)	0.78	0.86
	Ripening	0.89^{b} (± 0.02)	0.84	0.93
Ladybeetles	Tillering	0.82^{a} (± 0.01)	0.80	0.85
	Flowering	0.85^{a} (± 0.01)	0.84	0.87
	Ripening	0.94^{b} (± 0.01)	0.93	0.95

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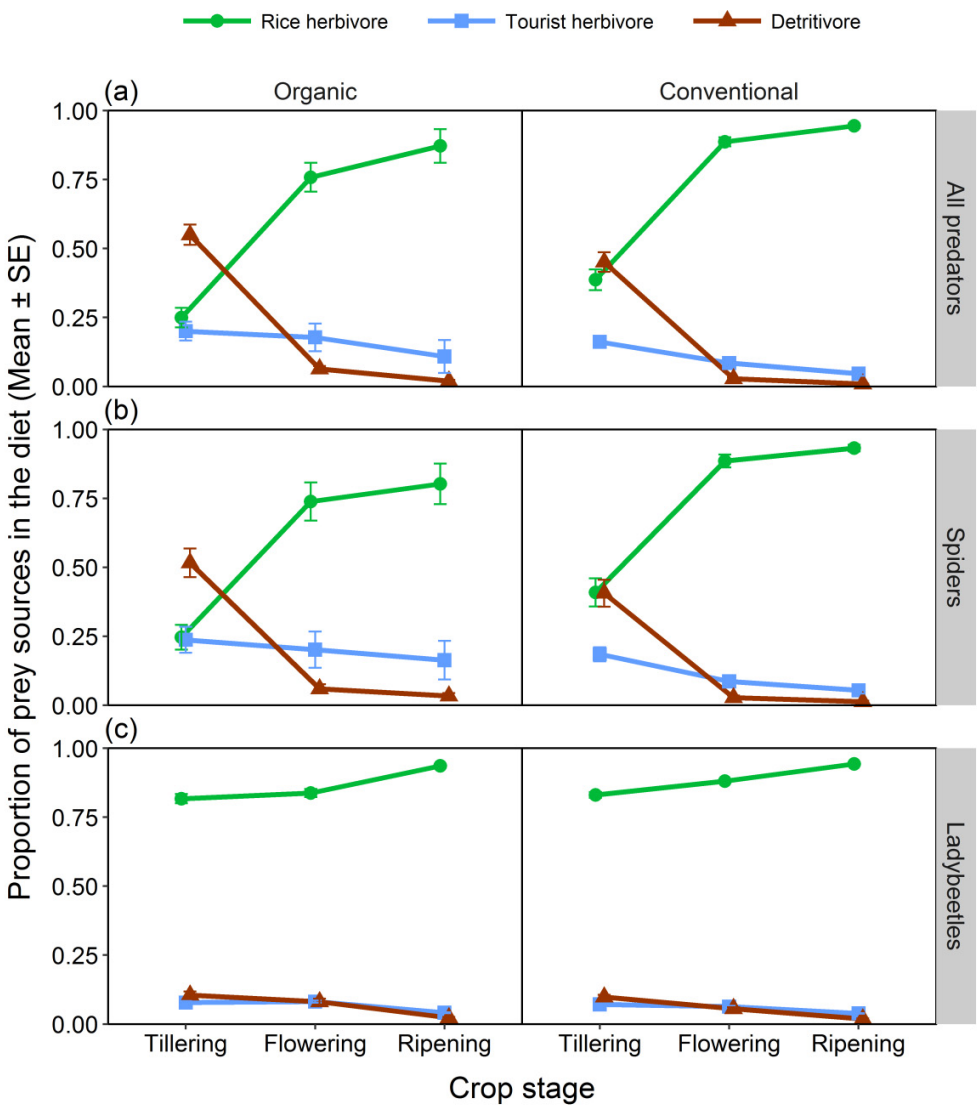

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558 **Figure 1.** The proportions (mean ± SE) of prey sources (rice herbivores, tourist herbivores, and
559 detritivores) consumed in the diet of (a) all predators, (b) spiders, and (c) ladybeetles in organic
560 and conventional rice farms over crop stages. The proportions were computed from the
561 Bayesian posterior means of replicate farms over three study years.

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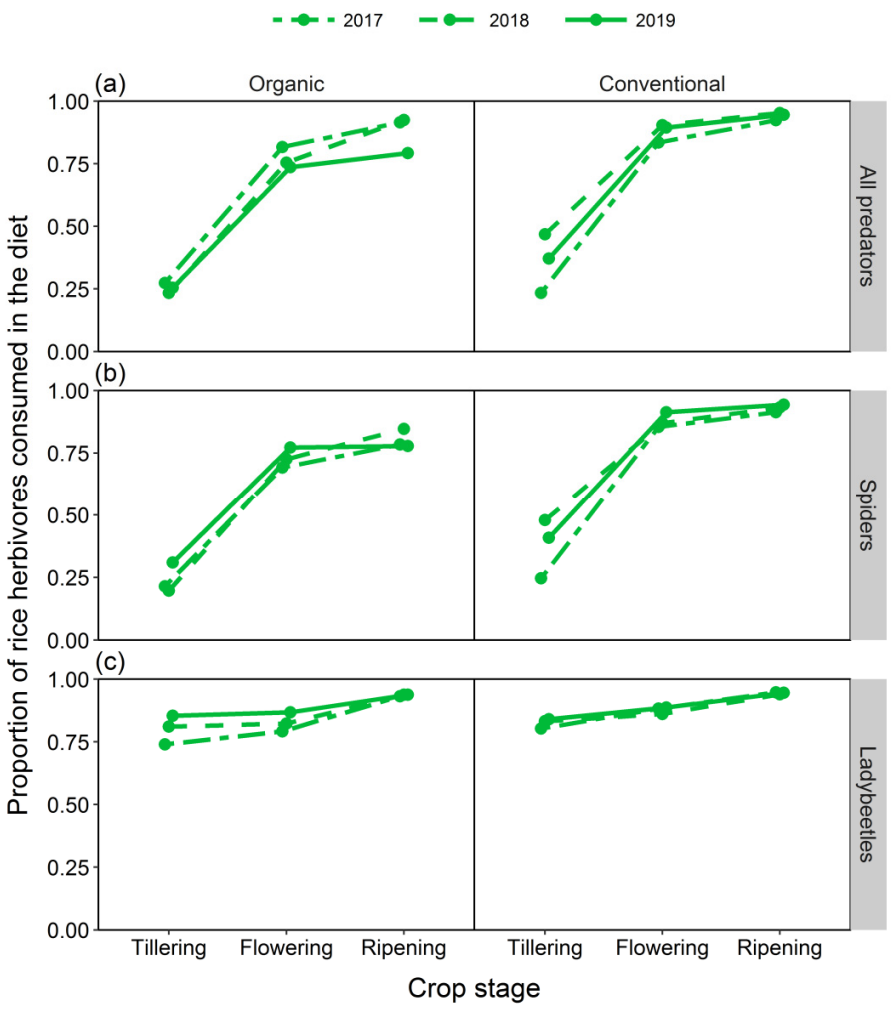

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564 **Figure 2.** The proportion of rice herbivores consumed in the diet of (a) all predators, (b) spiders,
565 and (c) ladybeetles in organic and conventional rice farms over crop stages in the three study
566 years. The proportions were computed from the Bayesian posterior means of replicate farms.

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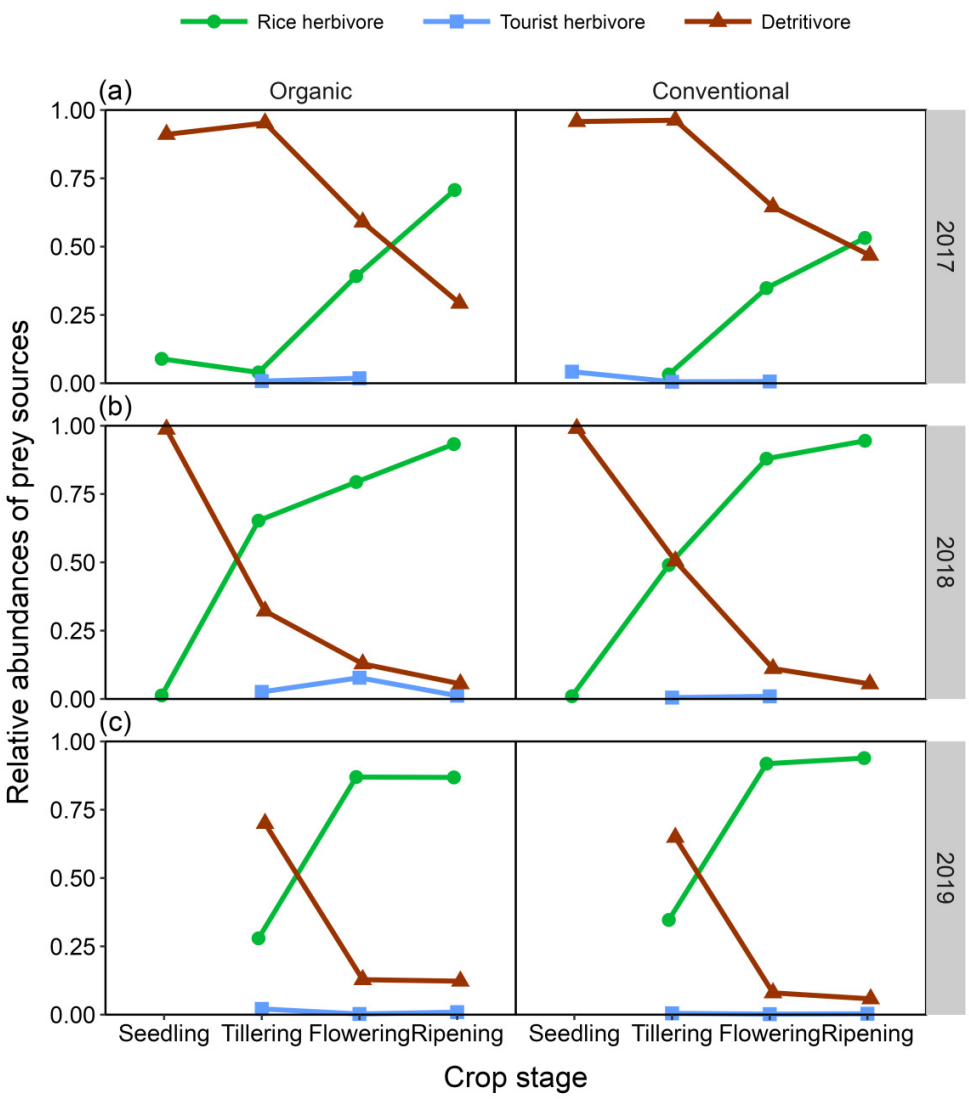

568

569 **Figure 3.** The relative abundance of prey sources in organic and conventional rice farms over
570 crop stages during the three study years. The relative abundance was determined from the
571 sweep-net samples pooled across replicate farms.